

STRUCTURAL VARIATION OF *OPHIOGOMPHUS MAINENSIS*:
DESCRIPTION OF A NEW SUBSPECIES AND RELATIONSHIP
TO SIBLING SPECIES (ODONATA: GOMPHIDAE)

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Abstract.—*Ophiogomphus mainensis mainensis* Packard, new status, consists of a large, stable population (New England and adjacent parts of New Jersey, Pennsylvania, New York, Quebec, and New Brunswick) and a disjunct population in the high mountains of North and South Carolina. An allopatric population in central Pennsylvania and West Virginia is named as a new subspecies *fastigiatus*. Structurally intermediate specimens from the vicinity of the boundary of the two ranges have been found in Pennsylvania and New York. *Ophiogomphus incurvatus* Carle may have been derived from *O. m. fastigiatus*, with the subspecies *O. i. alleghaniensis* Carle the bridging taxon. *Ophiogomphus acuminatus* Carle occurs southwest of these two species; its relation to the other two species is uncertain. The geographic pattern of variation of *O. mainensis* ssp. is unusual for odonates of the eastern United States, and is reminiscent of "leapfrog" variation of Andean birds.

The gomphid *Ophiogomphus mainensis* was described by Packard (1863) from a female collected in Maine. A male was determined as *mainensis* by Hagen (Selys, 1878; Howe, 1918); however, Howe's (1918) figure shows that it is not this species, and Garman (1927) identified it as *carolus* Needham. Needham (1897) reared a male of *mainensis* but described it as *O. johannus*. The two species *johannus* and *mainensis* were considered to be distinct until Garman (1927) established the synonymy.

The name *Ophiogomphus incurvatus* was proposed by Carle (1982) to replace the incorrectly named *O. carolinus* Hagen, a species of the piedmont of Georgia to Maryland. Carle also described the subspecies *O. i. alleghaniensis*, which occurs to the west of the nominate subspecies.

Ophiogomphus acuminatus was described by Carle (1981) from specimens from Tennessee. *O. bouchardi*, which was de-

scribed by Louton (1982), is a synonym. Although placed by Carle with *O. edundo* Needham, it seems to be closer to *O. mainensis* s. lat. and *incurvatus* s. lat.

The present study began with the recognition of a distinct taxon occurring in central and western Pennsylvania south to high elevations in West Virginia (Fig. 1). Although this taxon has some resemblance to *O. i. alleghaniensis*, it is closely related to *mainensis*. Preliminary studies suggested that it might merit specific status, but a few specimens of this taxon and typical *mainensis* close to their geographic boundary in northeastern Pennsylvania and southern New York show intermediate characters. Thus, the new taxon is considered a subspecies of *mainensis*.

Abbreviations for collectors' names in the descriptions are: TD = T. Donnelly; CS = C. Shiffer; HW = H. B. White III; FC = F. Carle; SD = S. Dunkle; CU = Cornell Univ.;

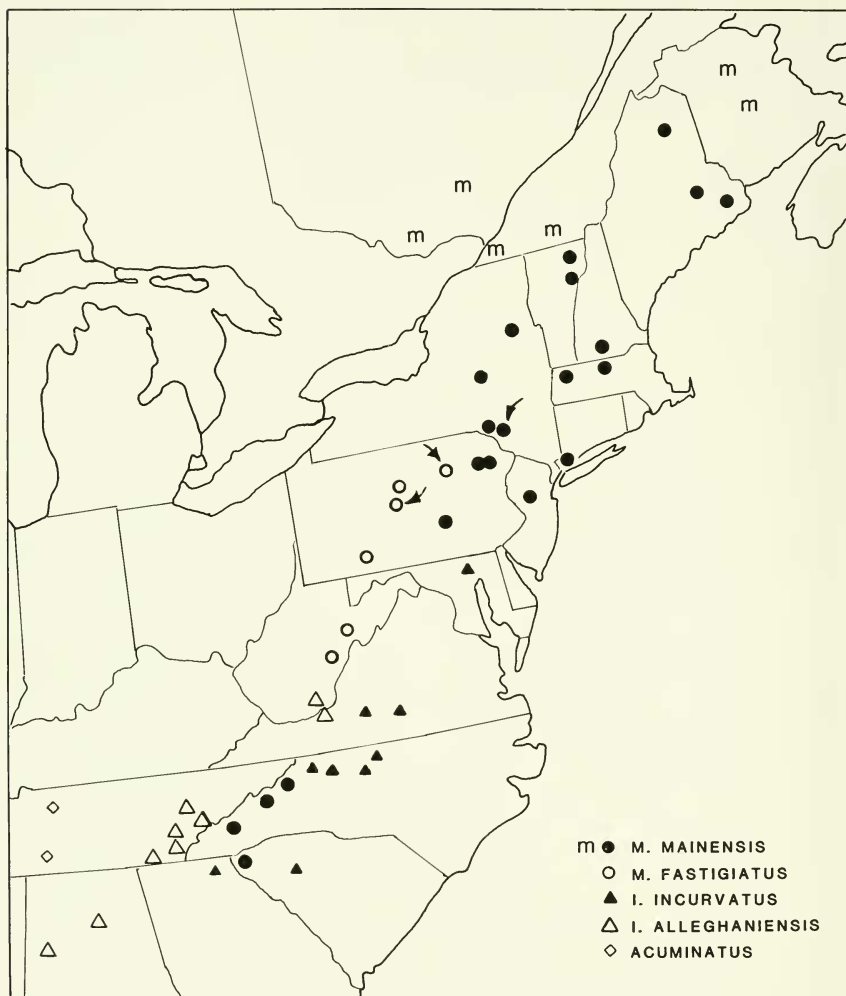


Fig. 1. Map showing distribution of *Ophiogomphus m. mainensis* (U.S. specimens examined for this study only; "m" for Canadian localities reported in Walker, 1958); *O. m. fastigiatus*; *O. i. incurvatus* (localities from Carle, 1982 and from my collection); *O. i. alleghaniensis* (localities from Carle, 1982, with additional localities from specimens in J. Louton Collection); and *O. acuminatus*. Arrows show localities with structurally intermediate specimens.

OF = O. S. Flint, Jr., U.S. Nat. Mus.; SB = S. W. Bromley, U.S. Nat. Mus.; ED = E. M. Davis, Mus. Comp. Zool.; EW = E. B. Williamson, Univ. Mich. Mus. Zool.

Ophiogomphus mainensis fastigiatus

Donnelly, NEW SUBSPECIES

Figs. 2-5

Ophiogomphus mainensis, Ahrens et al., 1968: 107. Butler Co. specimen included here.

Ophiogomphus mainensis, Beatty et al., 1969: 131. In part this subspecies.

Holotype male.—*Head*: pale yellow green, very dark brown as follows: thin marginal line on labrum, vertex except for a pale sub-basal medial spot.

Thorax: proepisternum very dark brown with pale lateral spots, proepimeron yellow brown. Pterothorax yellow green, with a very dark brown mid-dorsal line, which does not meet the anterior margin. Mesepisternum with a dark curved line extending to $\frac{5}{8}$ the distance to rear and not touching mesopleural suture. Mesopleural and metapleural sutures and margins of mesepimeron and metepisternum dark brown. Legs black except for obscure pale of coxae and interior surface of profemora.

Abdomen: Each segment mainly black, green as follows: sides of 1 and 2; basal-lateral and medial-lateral spots on 3 to 7, decreasing in size rearwards; fused lateral spots on 8 and 9; medial-basal lines on 1 to 8, thin and short on 3 to 8; tiny middorsal spot on 9; 10 with postero-lateral line and small posterior middorsal spot. Appendages brown, superiors indistinguishable from *m. mainensis*, in lateral view each appendage straight, tapering, divergent in dorsal view (Fig. 5, no. 11), sub-parallel sided in lateral view with prominent, small posteriorly directed apical point. Inferior appendage in lateral view with lateral spine low and less prominent than apical spine, located about $\frac{1}{2}$ the distance from base (Fig. 2, no. 9); in

ventral view (Fig. 3, no. 9) the appendage is distinctly wedge-shaped, in sharp contrast to typical *m. mainensis*, in which the appendage is obtusely truncated (Fig. 3, nos. 1 to 4).

Allotype female.—Coloration as in male, with pale colors slightly more extensive. The occiput with paired, anteriorly directed spines as in *m. mainensis*. The vulvar lamina resembles that of *m. mainensis*; in lateral view the tips are elevated and then deflected caudally, forming a sigmoid bend (Fig. 5, no. 10). A reliable distinction between females of *m. fastigiatus* and *m. mainensis* has not been found.

Types.—Holotype ♂, PENNSYLVANIA: Sullivan Co., Loyalsock Cr. 3 mi. N. of LaPorte, 4 July 1983 (TD). Allotype ♀, same loc., 19 June 1983 (TD). Paratypes: PENNSYLVANIA: same loc. as holotype: 19 June and 4 July, 5 ♂ 2 ♀ 1983 (TD and CS); Clinton Co., Kettle Cr., 2 mi. E. of Hammersley Fork, 21 June 1969, 21 June 1975, 22 June 1977, 25 June 1983, 5 ♂ 4 ♀ (CS); Centre Co., Black Moshannon Creek nr. Black Moshannon Dam, 4 Aug. 1983, 1 ♂ (CS); Somerset Co., Rockwood, 29 June 1900, 1 ♂ (EW); WEST VIRGINIA: Nicholas Co., Cranberry R. 5 mi. N. of Richwood (2100'), 25 June 1969, 1 ♂ (TD); Randolph Co., Shaver Fork of Cheat R. at highway 250 (3600'), 23 June 1973, 1 ♂ (HW). The holotype and allotype are deposited in the Florida State Collection of Arthropods.

Dimensions.—The holotype male has abdomen and appendages 34 mm long, and hind wing 26 mm long. The allotype female has these dimensions 32 and 27 mm. The total group examined (14 males, 7 females) has these dimensions 32.7 mm (.85) and 25.65 (.5) mm for the males and 31.8 (.4) and 27.1 (.7) for the females. The figure in parentheses is standard deviation.

Variations in the type series.—The color patterns show little variation. In about half the specimens the posterior end of the mesepisternal dark stripe is free, and in half it

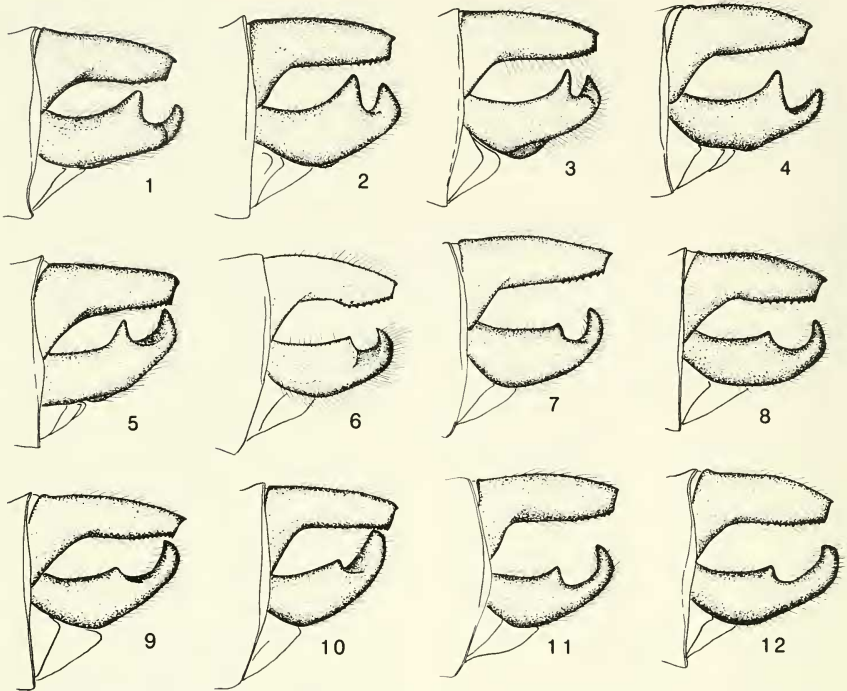


Fig. 2. Profiles of appendages of male *Ophiogomphus m. mainensis*, 1-5, and *O. m. fastigiatus*, 6-12. Specimens 5 (*mainensis*) and 6-8 (*fastigiatus*) show intermediate characteristics. Localities are 1 = Essex Co., Vt.; 2 = Perry Co., Pa.; 3 = Pike Co., Pa.; 4 = Haywood Co., N.C.; 5 = Sullivan Co., N.Y.; 6 and 7 = Sullivan Co., Pa.; 8 = Centre Co., Pa.; 9 = Sullivan Co., Pa. (holotype); 10 = Somerset Co., Pa.; 11 = Nicholas Co., W. Va.; 12 = Randolph Co., W. Va.

is fused with the humeral stripe. The three pale spots on abdominal segment 10 are fused in many specimens, forming a posterior band. The appendages show some variation, as seen in Figs. 2, 3, and 4. In three specimens (two from Sullivan Co., Pennsylvania, and one from Centre Co., Pennsylvania; Figs. 2 and 3, nos. 6 to 8) the lateral spine on the inferior appendage is set posterior to the midpoint, somewhat as in *m. mainensis*. Although these specimens are more like *m. fastigiatus* than *m. mainensis* in the ventral view of the appendages (Fig.

3, nos. 6 to 8) and in the relatively small medial spine of the inferior appendage, their intermediate character is significant.

Remarks.—The subspecies *m. fastigiatus* is distinguishable from the nominate subspecies by the form of the inferior appendage, which has a low, blunt lateral spine set at about the midpoint of the appendage (Fig. 2, nos. 9 to 12). In *m. mainensis* this appendage is variable, but always has a very prominent, pointed lateral spine located distinctly caudal to the mid point of the inferior appendage (Fig. 2, nos. 1 to 4). In

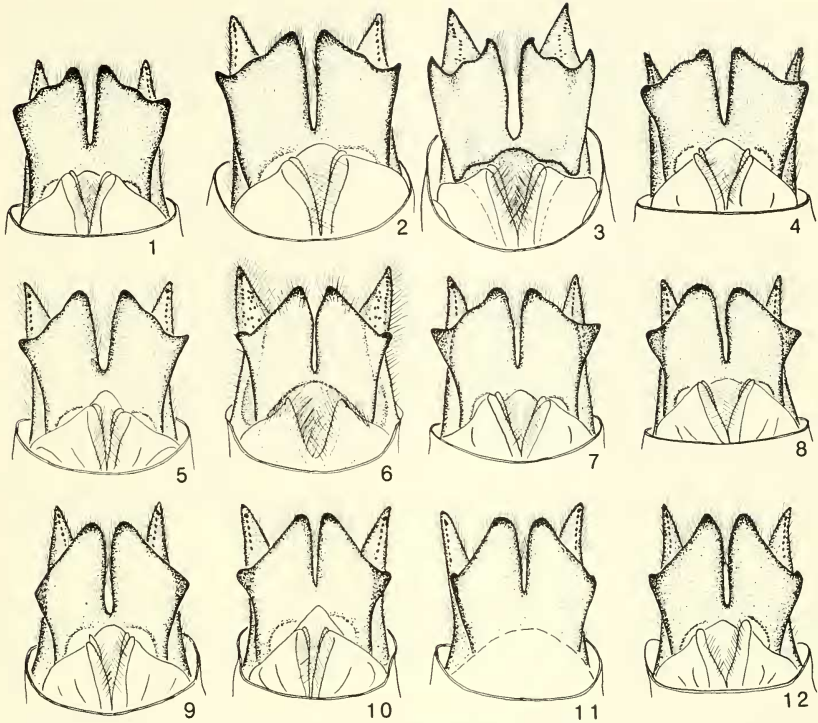


Fig. 3. Ventral views of male appendages of same specimens shown in Fig. 2.

ventral view (Fig. 3, nos. 9 to 12) the wedge of the inferior appendage is distinctive (the name *fastigiatus* refers to a gable).

Ophiogomphus mainensis mainensis

Packard, NEW STATUS

Figs. 2-4

Ophiogomphus mainensis, Packard, 1863.

Holotype ♀.

Ophiogomphus johannus, Needham, 1897.

Holotype ♂.

Ophiogomphus johannus, Howe, 1918.

Ophiogomphus mainensis, Garman, 1927.

Established synonymy of *mainensis* and *johannus*. Descr. ♂ and ♀, figs.

Ophiogomphus mainensis, Walker, 1958.

Descr. ♂ and ♀, figs.

Ophiogomphus mainensis, Carle 1982. Descriptive notes, figs.

The holotype is a female, which, as has been the case with many other gomphids, has resulted in continuing confusion. The male of the nominate subspecies has the thorax marked as follows: yellow green, with a dark brown mid-dorsal stripe ending posterior to anterior margin; dark brown stripes on mesopleural (humeral) and metapleural sutures, the latter covering the anterior half of suture; dark curved stripe on mesepisternum adjacent to mesopleural suture and

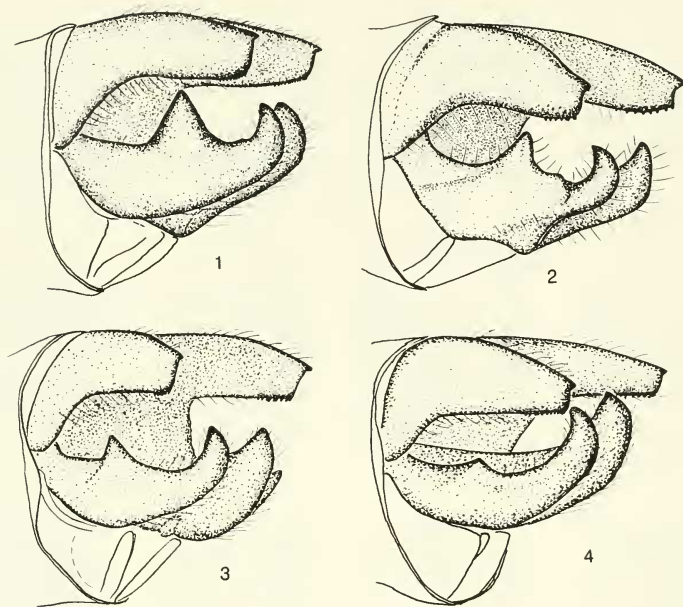


Fig. 4. Inclined views of male appendages of *O. m. mainensis*, 1–2, and *O. m. fastigiatus*, 3–4. Specimen 3 shows intermediate characteristics. Localities are 1 = Perry Co., Pa.; 2 = Pike Co., Pa.; 3 = Sullivan Co., Pa.; 4 = Sullivan Co., Pa. (holotype).

extending $\frac{2}{3}$ distance towards wing bases. The distinctive inferior appendage is shown in Figs. 2, 3, and 4.

Needham's holotype of *O. johannus* was examined and found to be *m. mainensis*. However, the holotype is a reared male preserved in alcohol, and the specimen has subsequently turned to a jellied mass, of which the sclerotized abdominal appendages are among the few portions recognizable as parts of an insect.

Material examined.—MAINE: Aroostook Co., 18 mi. W. Ashland, 19 July 1982, 1 ♂ (TD); Washington Co., E. Machias R. 3 mi. N. of Wesley, 11 July 1982, 2 ♂ (TD); Penobscot Co., Seboeis R. west of Shin Pond, 28 July 1959, 2 ♂ 1 ♀ (TD). MASSACHUSETTS: Franklin Co., West Hawley, 23 June 1971, 1 ♂ (HW); Middlesex Co.,

Ashby, 9 July 1939, 1 ♂ (ED). NEW YORK: Hamilton Co., nr. L. Durant, 3 July 1980, 1 ♂ 1 ♀ (HW); Herkimer Co., Wilmurt, n.d., 1 ♂ (holotype of *O. johannus*) (CU); Delaware Co., Beaver Kill, nr. Roscoe, 31 July 1967, 1 ♂ (TD); Sullivan Co., Beaver Kill at Lewbeach, 31 July 1967, 2 ♂ (somewhat intermediate to *fastigiatus*) (TD). VERMONT: Essex Co., nr. Island Pond, 14–15 July 1982, 5 ♂ 3 ♀ (SD); Brunswick, 7 July 1985, 1 ♂ 1 ♀ (HW); Outlet Dennis Pond, 24 June 1983, 2 ♂ (FC); Caledonia Co., Peacham, 27 June 1983, 2 ♂ (FC). NEW HAMPSHIRE: Hillsborough Co., Wilton, 22 June 1969, 1 ♂ (HW). CONNECTICUT: Fairfield Co., Stamford, 16 June 1940, 1 ♂ (SB). NEW JERSEY: Morris Co., Hacklebarney St. Pk., 21 June 1959, 1 ♂ (TD). PENNSYLVANIA: Pike Co., and Wayne

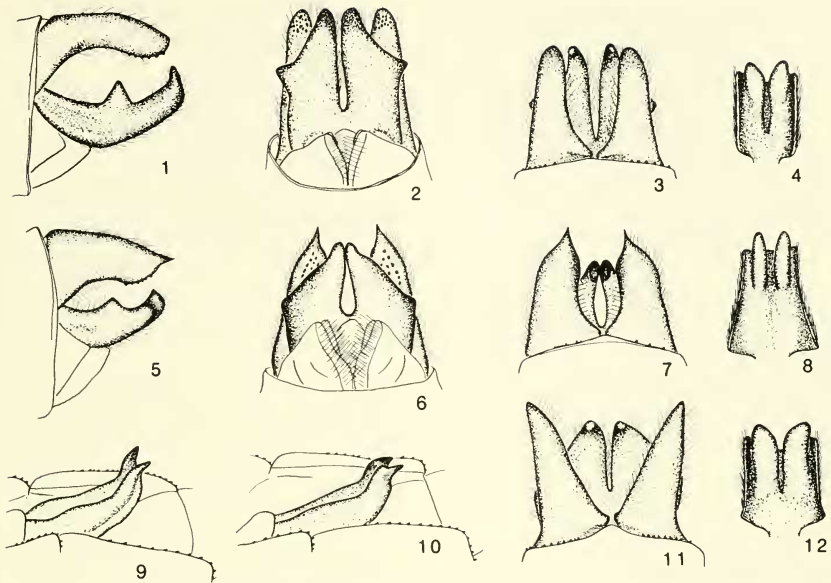


Fig. 5. Structural details of *Ophiogomphus incurvatus alleghaniensis*, 1-4, 9, *O. mainensis fastigiatus*, 10-12, and *O. acuminatus*, 5-8. 1 and 5 are lateral, 2 and 6 ventral, and 3, 7, and 11 are ventral views of male appendages. 9 and 10 are inclined views of female vulvar laminae. 4, 8, and 12 are the vesicle of the penis.

Co., nr. Greentown, 4-5 July 1985, 2 ♂ (TD); Perry Co., nr. New Bloomfield, 23 June 1965, 3-10 July 1966, 3 June 1975, 4 ♂ 1 ♀ (CS). NORTH CAROLINA: Haywood Co., nr. Sunburst, 15 June 1984, 2 ♂ (TD and CS); Yancey Co., nr. Busick, 11 June 1958, 6 ♂ (TD); Avery Co., nr. Minneapolis, 13 June 1958, 2 ♂ (TD). SOUTH CAROLINA: Oconee Co., Burrell's Ford, Chattooga R., 19 May 1970, 1 ♂ (OF).

Variations in *Ophiogomphus m. mainensis*.—Specimens from three disjunct populations were examined: a northern, extending from Maine to New Jersey and northeastern Pennsylvania (26 males, 6 females), a small group from Perry Co., Pennsylvania (4 males, 1 female), and a group from western North Carolina and South Carolina (11 males). Sizes of the three populations are virtually the same, and I de-

tected no distinction in color pattern nor structure between the northern and southern populations. The Perry Co. specimens were slightly larger but identical in coloration. The mean dimensions for males of the three groups of *m. mainensis* are as follows: northern group abdomens 32.4 (.6) mm and hind wings 25.7 (.6) mm; for the southern group 33.3 (.9) and 25.9 (.45) mm; for Perry Co., Pennsylvania 34.25 (.3) and 26.25 (.3) mm.

Remarks.—The two subspecies are indistinguishable in color pattern, and both show parallel variations in the mesepisternal dark stripe and pale color of segment 10. The sizes are very similar, except for the slightly larger Perry Co. population of *m. mainensis*.

The inferior appendages show some variation in the size of the lateral spine, but in

all specimens this spine is prominent, pointed, and located posterior to the mid point of the appendage. In ventral view the appendage varies from a nearly oblique termination to a more acute wedge shape. Two specimens from Sullivan Co., New York (Figs. 2, 3, no. 5) are extreme in this regard and appear to vary in the direction of *m. fastigiatus*, while still retaining a predominantly *m. mainensis* appendage.

In summary, the two subspecies *m. mainensis* and *m. fastigiatus* are allopatric with a tendency for structurally intermediate specimens to occur near the boundary between their ranges. The disjunct southern population is separated from West Virginia *m. fastigiatus* by a gap occupied by *Ophiogomphus incurvatus alleghaniensis*.

DISTINCTION AMONG TAXA OF THE *OPHIOGOMPHUS MAINENSIS* GROUP

The *Ophiogomphus mainensis* group contains three species (*mainensis*, *incurvatus*, and *acuminatus*), two of which have subspecies. Males of the three species are most readily identified by the form of the superior appendage (cerci), as shown in Fig. 5.

Ophiogomphus mainensis and *incurvatus* (Fig. 5, nos. 1-4) are distinguished by the pale femora, and rounded, blunt-tipped superior appendages of *incurvatus*. The inferior appendage viewed ventrally is wedge-shaped as in *m. fastigiatus* but has a prominent lateral spine as in *m. mainensis*. The abdomen is paler in *incurvatus* than in *mainensis*. The vesicle of the penis is black and broader in *mainensis* and narrower and centrally pale in *incurvatus*. The two subspecies of *incurvatus* have been characterized by Carle (1982). The similarity in the inferior appendages of *i. alleghaniensis* and *m. fastigiatus* is noteworthy and might have a bearing on their relationship. *Ophiogomphus acuminatus* is a lesser known species found in Tennessee. The male is readily distinguished by its broad superior appendage with a distinctively pointed tip (Fig. 5, nos.

5-7). The vesicle of the penis has narrower paired cylindrical processes than either *incurvatus* or *mainensis*.

Females of *mainensis* and *incurvatus* are best distinguished by the paler colors of the latter, as discussed by Carle (1982). The vulvar lamina of *i. alleghaniensis* (Fig. 5, no. 10) is similar to that of *m. fastigiatus* (Fig. 5, no. 9) but appears on the basis of one specimen to be distinguishable by its tip which is deflected ventrally rather than sigmoidally ventrally and caudally. However, this distinction may be a poor one; this sclerite is subject to both in vivo and post mortem changes in shape. The female of *acuminatus* has not been described.

Ophiogomphus m. mainensis and *m. fastigiatus* are allopatric and are distinguished from each other only by the form of the male inferior appendages (epiproct). Although this appendage shows some variability throughout both populations, all specimens examined are referable to one or the other subspecies by size of the lateral spine of the inferior appendage and by shape of this appendage in ventral view, as discussed above and shown in Figs. 2, 3 and 4. The existence in the boundary area between the subspecies of some specimens with appendages of intermediate shape shows that genetic isolation has not been achieved and reinforces the conclusion that the two taxa are of subspecific rank.

THE SYSTEMATIC RELATIONSHIPS AND PUTATIVE DERIVATION OF THE TAXA IN THE *OPHIOGOMPHUS MAINENSIS* GROUP

Ophiogomphus mainensis occurs from Quebec and New Brunswick southward in the high Appalachian Mountains to South Carolina, a distribution shared with many other Odonata. However, the subspecies *mainensis* occurs as two disjunct populations: the northern is widespread in New England, extending southward to Harrisburg at high elevations. The southern occupies the high mountains of western North and South Carolina. The subspecies *fasti-*

giatus occupies much of the intervening area, occurring from Pennsylvania south to the New River valley, which cuts through the Appalachians in southern West Virginia and southwestern Virginia. I suggest that *m. mainensis* is the ancestral form and originally had a continuous distribution throughout the entire range. This type of distribution is well known among Andean birds and has been called "leapfrog variation" by Remsen (1984), who suggested that the very young tectonics of the Andes might provide opportunities for restriction in gene flows, with the consequent appearance of derivative forms in the center of a once-continuous range.

The tentative explanation offered here begins with late Cenozoic uplift of the Appalachian mountains which was concentrated in the Carolinas along the Cape Fear arch. The uplift and accompanying westward tilting caused major tributaries of the Mississippi River system (Tennessee, French Broad, Holston, and New rivers) to penetrate the mountains and capture former eastward drainages. Continued development of these river systems left the Appalachian chain divided into segments. The New River created the broadest low-elevation division of the mountain chain. Subsequent to Pleistocene glaciation, odonate species in a putative southern Appalachian refugium spread northward along the mountain chain. Continued amelioration of the climate drove many species into higher areas, and the gaps created by cross-cutting river systems left some of these populations genetically isolated. The originally continuous population of *Ophiogomphus mainensis* was broadly divided by the New River gap. One possible result was the appearance of a relatively low-elevation form (*O. mainensis fastigiatus*) in this gap. Further climatic amelioration drove the boundary between *mainensis* and *fastigiatus* further north to its present position, where the two subspecies face each other across a relatively short boundary region.

At a still later time, a new form, *O. incurvatus*, supplanted *fastigiatus* at lower elevations in this gap. It subsequently divided into two forms, *i. incurvatus* and *i. alleghaniensis*, across the drainage divide between the New and Roanoke River systems in southwestern Virginia. At present *i. incurvatus* is confined to Atlantic drainages, and *i. alleghaniensis* occupies Gulf and Mississippi drainages. The origin of *acuminatus* remains elusive, but a derivation from *incurvatus* is plausible. The similarity between the inferior appendages of *m. fastigiatus* and *i. alleghaniensis* is consistent with these taxa being annectant forms between the two species but is not compelling. Other schemes might be proposed; a final resolution of this question would best be approached through an assessment of protein similarities.

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